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Synthesis and modeling perspectives of rhizosphere priming

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Summary

The rhizosphere priming effect (RPE) is a mechanism by which plants interact with soil functions. The large impact of the RPE on soil organic matter decomposition rates (from 50% reduction to 380% increase) warrants similar attention to that being paid to climatic controls on ecosystem functions. Furthermore, global increases in atmospheric CO_2 concentration and surface temperature can significantly alter the RPE. Our analysis using a game theoretic model suggests that the RPE may have resulted from an evolutionarily stable mutualistic association between plants and rhizosphere microbes. Through model simulations based on microbial physiology, we demonstrate that a shift in microbial metabolic response to different substrate inputs from plants is a plausible mechanism leading to positive or negative RPEs. In a case study of the Duke Free-Air CO_2 Enrichment experiment, performance of the PhotoCent model was significantly improved by including an RPE-induced 40% increase in soil organic matter decomposition rate for the elevated CO_2 treatment – demonstrating the value of incorporating the RPE into future ecosystem models. Overall, the RPE is emerging as a crucial mechanism in terrestrial ecosystems, which awaits substantial research and model development.

I. Introduction

Plant–soil interactions play a central role in terrestrial ecosystem functions. These interactions often occur in the rhizosphere, and, thus, are generally referred to as rhizosphere interactions. Rhizosphere interactions, at the global scale, may control as much as 50% of the total CO_2 released from terrestrial ecosystems (Schimel, 1995; Hopkins *et al.*, 2013) and regulate virtually all aspects of

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nutrient cycling (e.g. Chapin *et al.*, 2011). One crucial component of these rhizosphere interactions is the rhizosphere priming effect (RPE), which is defined as the stimulation or suppression of soil organic matter (SOM) decomposition by live roots and associated rhizosphere organisms when compared to SOM decomposition from rootless soils under the same environmental conditions. Recent research suggests the RPE has the potential to alter SOM dynamics. A fundamental understanding of the processes that govern the turnover of SOM, the largest terrestrial reservoir of organic carbon (C), is critical to predicting biospheric feedbacks to the global C cycle and climate change (Heimann & Reichstein, 2008). At the global scale, CO_2 released by SOM decomposition is one of the key processes that determine the overall magnitude of C storage in terrestrial ecosystems. Over the past decade emerging evidence indicates that the RPE may play a crucial role in regulating C inputs to SOM and its turnover (e.g. Cheng & Kuzyakov, 2005; Phillips *et al.*, 2012). These findings have stimulated a recent interest in incorporating roots and root–microbe interactions into ecosystem and Earth system models (Ostle *et al.*, 2009).

Despite the emerging view that roots are an integral component of soil function and that root–microbe interactions such as the RPE may be of equal or greater importance than aboveground factors in coupling C and nutrient cycles (Frank & Groffman, 2009), remarkably little is known about the biogeochemical consequences of the RPE (Bird *et al.*, 2011; Gärdenäs *et al.*, 2011). Further, because most SOM models were developed by using data from experiments with root-free soils, the role of the RPE in shaping ecosystem and global biogeochemical models has been neglected. The overall objective of this paper is to synthesize research on the RPE. We first review the magnitude of the RPE, and the effects of global change factors on the RPE. We then consider whether the RPE is an evolutionarily stable strategy by using a game theoretic model and explore the relative importance of substrate quality and quantity on the RPE via a model based on microbial physiology. Next, in a case study using results from the Duke Free-Air CO_2 Enrichment (FACE) experiment, we evaluate whether inclusion of the RPE into PhotoCent, a revised version of the ForCent ecosystem model (Parton *et al.*, 2010), can improve the match between model simulations and experimental observations. Lastly, we discuss the research needs and future perspectives for explicitly incorporating the RPE into SOM and ecosystem models.

II. Magnitude and driving variables of the rhizosphere priming effect

Published results from experimental studies in plant growth chambers and glasshouses indicate that the magnitude of the RPE varies widely, ranging from 380% enhancement to 50% reduction as compared to basal respiration from root-free soils (Table 1). These levels of the RPE demonstrate that rhizosphere processes are major drivers of SOM mineralization. Yet, the RPE does not necessarily result in an ultimate decline of total SOM because the overall input of organic materials from the rhizosphere may compensate for the enhanced mineralization of accessible SOM (Cheng, 2009). These results also indicate that the RPE can be significantly influenced by both plant and soil variables.

Among plant variables, different plant species tend to produce significantly different RPE values. For instance, the RPE of soybean (*Glycine max*) was consistently higher than that of wheat (*Triticum aestivum*) when both species were grown in the same soil under the same environmental conditions (Fu & Cheng, 2002; Cheng *et al.*, 2003). Similarly, ponderosa pine (*Pinus ponderosa*) produced a much larger RPE than Fremont cottonwood (*Populus fremontii*) (Dijkstra & Cheng, 2007b), and Sitka spruce (*Picea sitchensis*) primed SOM mineralization significantly more than ponderosa pine or Western hemlock (*Tsuga heterophylla*) (Bengtson *et al.*, 2012). Although the quality and quantity of root exudates are thought to be key plant traits controlling the RPE (Kuzyakov, 2010), the actual traits responsible for the large observed differences in RPE are virtually unknown. An unstudied but potentially important influence of plant species on the realized level of RPE is root architecture because it largely determines rhizosphere surface area per unit of root biomass. Mycorrhizal partners, which vary in their associations with different plant species, also can be important in determining the RPE (Phillips & Fahey, 2006; Cheng *et al.*, 2012). In addition to species-level controls, canopy photosynthetic activity and photo-assimilate supply are intimately coupled to the RPE, with time lags as short as 48 h in the case of young annual crops (Kuzyakov & Cheng, 2001, 2004). Further, plant phenology can modulate the RPE. For example, in studies with crop species, the RPE was small when plants were young, tended to reach the highest level during early flowering stage, and declined afterwards (Cheng *et al.*, 2003; Cheng & Kuzyakov, 2005). These laboratory results generally indicate that plant variables can substantially control and influence the magnitude of the RPE.

Soil variables also can influence the RPE, even though they have been less studied. Significantly different levels of RPE can occur when the same plant species is grown in different soils (Dijkstra & Cheng, 2007b). For example, soybean (*Glycine max*) and sunflower (*Helianthus annuus*) grown in an agricultural soil resulted in a RPE of 60% but did not induce a significant RPE when grown under the same environmental conditions in soil from a nearby annual grassland (Dijkstra *et al.*, 2006). However, it is not clear which soil properties lead to differences in the RPE, and this subject needs further investigation. Some studies have suggested that high N availability may enhance the RPE (Hoosbeek *et al.*, 2006; Rasmussen *et al.*, 2007), but others have reported a larger RPE in soils with greater N limitation (Fontaine *et al.*, 2004). Nitrogen fertilization was initially thought to reduce the intensity of the RPE (Liljeroth *et al.*, 1994). However, a later study showed that the RPE can also increase with N fertilization (Cheng & Johnson, 1998). Both soil water content (Dijkstra & Cheng, 2007a) and drying–wetting cycles (Zhu & Cheng, 2013) were identified as important variables for controlling the RPE. To date, all investigated soil variables appear to have some influence on the RPE, but their relative importance is largely unknown. Furthermore, many potentially critical aspects of soil controls on the RPE (e.g. biological communities, texture, mineralogy, structure and chemical composition) have not been explored. Hence, the above-mentioned results may only represent a few initial pieces of an extremely complex puzzle that must be solved to gain an overall understanding of how soils influence the RPE.

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Table 1 Rhizosphere priming effects as measured by isotope methods under controlled laboratory or glasshouse conditions (updated from Cheng & Kuzyakov, 2005; Zhu & Cheng, 2011)

Plant Type	Treatment	Soil[1]	PGC[2]	%Priming[3]	Time[4] (d)	Reference
Zea mays		SLG	GC	236	25	Helal & Sauerbeck (1984)
Zea mays		SLG	GC	332	30	Helal & Sauerbeck (1986)
Zea mays	High N	LS	GC	133	47	Liljeroth *et al.* (1994)
Triticum aestivum	High N	LS	GC	33	47	Liljeroth *et al.* (1994)
Zea mays	Low N	LS	GC	196	47	Liljeroth *et al.* (1994)
Triticum aestivum	Low N	LS	GC	196	47	Liljeroth *et al.* (1994)
Triticum aestivum		CLO	GC	−37	16	Cheng (1996)
Triticum aestivum	Ambient CO_2	CLK	GC	44	28	Cheng & Johnson (1998)
Triticum aestivum	Elevated CO_2	CLK	GC	17	28	Cheng & Johnson (1998)
Triticum aestivum	Ambient CO_2, +N	CLK	GC	42	28	Cheng & Johnson (1998)
Triticum aestivum	Elevated CO_2, +N	CLK	GC	73	28	Cheng & Johnson (1998)
Helianthus annuus	Ambient CO_2	CLK	GH	55	53	Cheng *et al.* (2000)
Helianthus annuus	Elevated CO_2	CLK	GH	31	53	Cheng *et al.* (2000)
Triticum aestivum	12 : 12 h light : dark	CLK	GC	100	38	Kuzyakov & Cheng (2001)
Triticum aestivum	12 : 60 h light : dark	CLK	GC	−50	38	Kuzyakov & Cheng (2001)
Zea mays	12 : 12 h light : dark	SLC	GC	−31	19	Kuzyakov & Cheng (2004)
Zea mays	12 : 60 h light : dark	SLC	GC	NS[5]	19	Kuzyakov & Cheng (2004)
Glycine max	Growing season mean	CLK	GH	70	120	Fu & Cheng (2002)
Helianthus annuus	Growing season mean	CLK	GH	39	120	Fu & Cheng (2002)
Sorghum bicorlor	Growing season mean	SLC	GH	NS	120	Fu & Cheng (2002)
Amaranthus hypochondriacus	Growing season mean	SLC	GH	NS	120	Fu & Cheng (2002)
Glycine max		CLK	GH	NS	35	Cheng *et al.* (2003)
Triticum aestivum		CLK	GH	NS	35	Cheng *et al.* (2003)
Glycine max		CLK	GH	382	68	Cheng *et al.* (2003)
Triticum aestivum		CLK	GH	287	68	Cheng *et al.* (2003)
Glycine max		CLK	GH	312	89	Cheng *et al.* (2003)
Triticum aestivum		CLK	GH	130	89	Cheng *et al.* (2003)
Glycine max		CLK	GH	254	110	Cheng *et al.* (2003)
Triticum aestivum		CLK	GH	60	110	Cheng *et al.* (2003)
Glycine max	Growing season mean	CLK	GH	164	119	Cheng *et al.* (2003)
Triticum aestivum	Growing season mean	CLK	GH	96	119	Cheng *et al.* (2003)
Glycine max	Farm soil	SLC	GC	59	54	Dijkstra *et al.* (2006)
Helianthus annuus	Farm soil	SLC	GC	62	54	Dijkstra *et al.* (2006)
Glycine max	Nearby grassland soil	SLC	GC	NS	54	Dijkstra *et al.* (2006)
Helianthus annuus	Nearby grassland soil	SLC	GC	NS	54	Dijkstra *et al.* (2006)
Helianthus annuus	45% field H_2O capacity	SLC	GH	52	69	Dijkstra & Cheng (2007a)
Helianthus annuus	85% field H_2O capacity	SLC	GH	76	69	Dijkstra & Cheng (2007a)
Populus fremontii		CLK	GH	102	340	Bader & Cheng (2007)
Pinus ponderosa		SLC	GH	114	395	Dijkstra & Cheng (2007b)
Populus fremontii		SLC	GH	54	395	Dijkstra & Cheng (2007b)
Pinus ponderosa		FHP	GC	156	6#	Bengtson *et al.* (2012)
Picea sitchensis		FHP	GC	244	6#	Bengtson *et al.* (2012)
Tsuga heterophylla		FHP	GC	152	6#	Bengtson *et al.* (2012)
Helianthus annuus	Soil warmed by 2.7°C	SLC	GC	136	51	Zhu & Cheng (2011)
Helianthus annuus	Soil unwarmed	SLC	GC	115	51	Zhu & Cheng (2011)
Helianthus annuus	Soil warmed by 4.5°C	SLC	GC	78	57	Zhu & Cheng (2011)
Helianthus annuus	Soil unwarmed	SLC	GC	47	57	Zhu & Cheng (2011)
Helianthus annuus	Soil warmed by 5.0°C	SLC	GC	39	50	Zhu & Cheng (2011)
Helianthus annuus	Soil unwarmed	SLC	GC	17	50	Zhu & Cheng (2011)
Glycine max	Soil warmed by 5.0°C	SLC	GC	58	50	Zhu & Cheng (2011)
Glycine max	Soil unwarmed	SLC	GC	27	50	Zhu & Cheng (2011)
Glycine max	With nodules	SLC	GH	53	73	Zhu & Cheng (2012)
Glycine max	Without nodules	SLC	GH	26	73	Zhu & Cheng (2012)
Helianthus annuus	Constant moisture	SLC	GH	69	68	Zhu & Cheng (2013)
Helianthus annuus	Severe drying-wetting cycles	SLC	GH	33	68	Zhu & Cheng (2013)
Glycine max	Constant moisture	SLC	GH	82	68	Zhu & Cheng (2013)
Glycine max	Moderate drying-wetting cycles	SLC	GH	85	68	Zhu & Cheng (2013)

[1]Soil: LS, loamy sand (the Netherlands); SLG, Sandy loam (Germany); CLO, clay loam (Ohio, USA); CLK, clay loam (Kansas, USA); SLC, sandy loam (California, USA); FHP, ferro-humic podzol (British Columbia, Canada).
[2]Plant growth conditions: GH, glasshouse; GC, growth chamber.
[3]Each value is calculated as: (planted − unplanted)/unplanted × 100.
[4]Time: days after planting
[5]NS, no significant difference between the planted treatment and the unplanted treatment.
#pulse-chase labeling.

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Temporal scales associated with the RPE are also important to consider. The duration of the experiments summarized in Table 1 ranged from 16 to 395 d. All negative RPEs were reported from experiments of short duration (16–38 d), which suggests that negative RPEs may not persist or are associated primarily with the initial soil disturbance. For the positive RPEs in Table 1, the persistence of the RPE remains an open question. On the basis of results from short-term laboratory experiments, the priming effect has been viewed as relating primarily to mineralization of labile SOM (Kuzyakov *et al.*, 2000), and therefore its persistence might depend on the size and turnover time of the labile SOM pool. However, recent results indicate that priming may actually accelerate the decomposition of stabilized SOM and even black carbon, possibly due to the alleviation of microbial energy limitations (Hamer *et al.*, 2004; Fontaine *et al.*, 2007; Kuzyakov *et al.*, 2009). In fact, during a 395-d continuous labeling experiment (Dijkstra & Cheng, 2007b), the RPE of small trees did not decline as the labile SOM pool diminished. Instead, the RPE continued well after initial soil disturbance and throughout the entire experiment, demonstrating directly that the RPE can be a persistent phenomenon. Some field experiments using FACE technology further imply the potential continual nature of the RPE (Allard *et al.*, 2006; Langley *et al.*, 2009; Drake *et al.*, 2011). Thus, the RPE could be particularly relevant to the dynamics of stabilized SOM (Clemmensen *et al.*, 2013), and incorporation of the RPE into ecosystem and Earth system models might improve model performance for predicting long-term changes in SOM.

Overall, the RPE emerges as a key mechanism in mobilizing (Table 1) and possibly also stabilizing (Jastrow *et al.*, 2000; Clemmensen *et al.*, 2013) SOM, forming a key link between plant functions and soil functions in terrestrial ecosystems. Yet, many research questions remain. How sensitive is the RPE to global environmental change such as warming, elevated CO_2, and N deposition? Is the RPE a consequence of evolutionary processes between plants and soil microorganisms that renders benefits to both? How can both positive and negative RPEs (Table 1) be reconciled? Can a change in soil microbial physiology switch a positive RPE to a negative one and *vice versa*? If the RPE can potentially modulate soil biogeochemical processes to a large degree (as shown in Table 1), to what extent can our current SOM models be improved by incorporating the RPE? These exploratory questions are addressed in the following sections.

III. Will global environmental change alter the RPE?

As indicated in the previous section, global change drivers (e.g. warming, rising atmospheric CO_2 concentration, N deposition) can significantly alter the RPE (Table 1). At the global scale, even a small shift in the magnitude of the RPE has the potential to outweigh the effects of global change drivers on basal SOM decomposition in many ecosystems. Thus, critical consideration is needed to determine the value of representing rhizosphere processes and rhizosphere feedbacks in Earth system models. For example, if climate warming disproportionally stimulates microbial decomposition, the extra CO_2 efflux from SOM mineralization may cause further warming (Jenkinson *et al.*, 1991; Bond-Lamberty & Thompson, 2010). The strength of this positive feedback depends largely on the realized temperature sensitivity of SOM decomposition (Hopkins *et al.*, 2013). Because RPE-driven SOM decomposition is naturally entangled with basal soil respiration, it is critical to evaluate the temperature sensitivity of the RPE in reference to the temperature sensitivity of basal soil respiration, given the substantial contribution of the RPE to total soil CO_2 efflux (Table 1).

In most field-warming experiments, temperature sensitivity observations are based on total belowground CO_2 efflux, which includes both the rhizosphere component and the component of SOM decomposition. The two components may respond to warming in different ways (Boone *et al.*, 1998; Hartley *et al.*, 2007). The autotrophic component is often tightly coupled with photosynthesis (Högberg *et al.*, 2001; Tang *et al.*, 2005; Gomez-Casanovas *et al.*, 2012) and is controlled largely by plants, often showing a transient response to temperature change (Tjoelker *et al.*, 1999; Moyano *et al.*, 2007). For this reason, the real temperature sensitivity of SOM decomposition is obscured by the rhizosphere component in many field experiments (Bader & Cheng, 2007). Studies using laboratory soil incubations exclude the rhizosphere component, implicitly assuming that rhizosphere processes have little influence on SOM decomposition rates. However, this assumption is often invalid because the RPE frequently can be large in magnitude as indicated by the results summarized in Table 1. Although much research has been carried out in the past few decades, the issue concerning the temperature sensitivity of SOM decomposition remains controversial (Davidson & Janssens, 2006; Subke & Bahn, 2010). Some studies have shown that an increase in temperature may accelerate SOM decomposition (e.g. Trumbore *et al.*, 1996; Holland *et al.*, 2000). By contrast, other studies have indicated either transient or insensitive responses of SOM decomposition to temperature changes (e.g. Giardina & Ryan, 2000; Luo *et al.*, 2001; Melillo *et al.*, 2002). Overlooking the important role of rhizosphere interactions may be one of the possible causes of this controversy (Langley *et al.*, 2005; Reichstein *et al.*, 2005).

The magnitude of rhizosphere effects on SOM mineralization could be large enough to substantially shift the realized temperature sensitivity of SOM decomposition, particularly if temperature influences the magnitude of the RPE. The results from mesocosm studies of a model grassland ecosystem (Verburg *et al.*, 2004, 2005) indicate a higher temperature response of the rhizosphere effect, because the diurnal variation of SOM decomposition rates increases with increasing rhizosphere input. Studies using soil trenching to quantify root contributions to soil CO_2 efflux in temperate hardwood forest also suggest that the RPE could play a role in the temperature sensitivity of SOM decomposition (Boone *et al.*, 1998; Epron *et al.*, 1999). In these studies, the presence of roots increased the Q_{10} value for soil CO_2 efflux compared to the 'root-free' soil, and the RPE may have contributed to this difference, even though seasonal root dynamics and rhizosphere respiration were certainly major direct contributing factors. But, without an independent measurement of the RPE, its exact role in shaping the temperature sensitivity of SOM decomposition cannot be determined. Results from a plant growth chamber study

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(Zhu & Cheng, 2011) did, however, directly demonstrate that soil warming by 5°C magnified the RPE up to three-fold and that the overall temperature sensitivity of SOM decomposition was consistently enhanced by the RPE. Thus, a better understanding of how the RPE will respond to climate warming at different spatial and temporal scales is needed to determine its potential for improving predictions of climate–carbon cycle feedbacks and other related Earth system functions.

Results from multiple CO_2-enrichment experiments suggest that the RPE is an important driver of soil organic C (SOC) dynamics and ecosystem productivity. In a mesocosm study with several tree species at the Duke Forest FACE site, elevated CO_2 significantly increased total soil respiration while simultaneously reducing soil sequestration of root-derived C (Phillips *et al.*, 2012). In a *Populus deltoides* plantation, elevated CO_2 significantly increased rhizosphere C input, leading to a 10–20-fold increase in SOM decomposition (Trueman & Gonzalez-Meler, 2005). Elevated CO_2 significantly reduced SOC storage after 6 yr in a scrub-oak ecosystem despite higher plant growth and possibly higher rhizosphere C input (Carney *et al.*, 2007; Langley *et al.*, 2009). In each of these studies, the RPE was invoked as a possible mechanism for accelerating SOC loss but the role of the RPE in ecosystem processes was not described explicitly. Before the empirical results generated by FACE experiments, the prevailing hypothesis was that elevated-CO_2 stimulation of net primary production (NPP) would enhance litter and root detrital inputs to soils and thereby increase SOC storage (Norby *et al.*, 2002). Although increases in SOC were seen at some sites (e.g. Jastrow *et al.*, 2005; Hoosbeek & Scarascia-Mugnozza, 2009), results from other FACE studies failed to support this hypothesis, as increased belowground inputs of C under elevated CO_2 had no measurable effects on SOC accumulation in the mineral soil (Allard *et al.*, 2006; Talhelm *et al.*, 2009; Drake *et al.*, 2011). Further, at the Duke FACE site, mature loblolly pine trees exposed to elevated CO_2 significantly increased root exudation rates by up to 55% leading to an increase in the activity of exoenzymes that mobilize N (Phillips *et al.*, 2011). This increase in exudation was coupled with an increase in belowground C allocation that promoted N uptake (Drake *et al.*, 2011). Thus, the RPE appears to be a key mechanism that regulates the response of the terrestrial C cycle to elevated CO_2 through it impacts on SOM decomposition and the availability of N to support primary production (Billings *et al.*, 2010).

Effects of other global change drivers on the RPE have been less studied. However, the degree to which N deposition influences SOC pools is also likely to depend on the RPE. It is widely known that plants decrease belowground C allocation in response to N enrichment, and that in some cases this may lead to decreases in exudation (Phillips *et al.*, 2009) and reductions in the RPE (Phillips & Fahey, 2006). Therefore, the intensity of the RPE elicited by roots may depend on the availability of N. If N is highly available, plants may downregulate their root exudate production and, as a result, the RPE is much reduced. But, if N becomes limiting (as is often the case with elevated CO_2), the intensity of the RPE would increase. However, this N-limitation hypothesis needs further testing. Overall, how the RPE may respond to environmental variables warrants further studies.

IV. A game theoretic model: is priming the result of evolutionarily stable strategies?

Root exudation rates can vary greatly among species (Table 1; Grayston *et al.*, 1996; Jones *et al.*, 2009). However, little is known about which plants induce priming and which do not. This represents a critical knowledge gap for modeling the RPE. Variations in the RPE among species in a population may lead to interesting outcomes in terms of plant and microbial co-evolution. We explored the interactions between priming and nonpriming plants in a game theoretic model. While it is possible that the RPE is a by-product of passive leaching of C exudates from the plant, it has also been hypothesized that the RPE is an evolutionarily developed mechanism of indirect symbiosis or mutualism between plants and rhizosphere microorganisms (e.g. Denison *et al.*, 2003; Lambers *et al.*, 2009). Within this context of co-evolution, plant-derived labile C benefits rhizosphere microorganisms, who in turn mobilize pools of nutrients, benefitting the plants (Fig. 1a). This evolutionary hypothesis is often stated, but the conditions that may lead to the evolution of priming and priming effects are not known. Although this mutualistic explanation is appealing, like many cooperative associations it may be open to parasitism from 'free riders' with cheating strategies that do not contribute to the mutualistic benefits (Denison *et al.*, 2003). The mutualism involved in the RPE may be particularly open to parasitism or cheaters because, unlike other plant–microbe associations (e.g. N-fixation or mycorrhizal associations), the microbes involved in the RPE are not physically integrated with the plant. This means that the plant must broadcast C compounds into the soil, where they may be intercepted either by cooperating microbes or by cheating microbes that defect from the mutualism (Fig. 1b). The microbes must also release nutrients freely into the soil solution, where they may be intercepted by priming plants, by nonpriming plants (Fig. 1b) or even by a variety of other microbial competitors. A basic exploration of the factors that may or may not favor the evolution of this mutualism would be invaluable for generating hypotheses about the RPE.

Consider a hypothetical plant population that contains two types of plants that differ in priming strategies (Fig. 1b). One type produces root exudates that stimulate rhizosphere microorganisms and may gain access to plant-unavailable nutrients depending on the activities of the microbes. We imagine these to be inaccessible soil-bound N or phosphorus, but they could be any soil resource that is limiting to plant growth and is made available to plants through a RPE. A second type does not produce root exudates but still might gain access to a portion of the resources which are mobilized by microbial activities if their rhizosphere neighbors engage in soil priming (Fig. 1b). These two types of plants interact with a population of rhizosphere microorganisms that also contains two strategies (Fig. 1b). One cooperates with plants by taking root exudates and using some of them to mobilize a portion of the soil nutrients which may then be captured by plants. The other defects from the mutualism by taking the root exudates but providing nothing to the plant in return (Fig. 1b). In this game theoretic model, priming plants gain nothing if the microbes are defecting, and cooperating microbes gain nothing if the plants do not engage in rhizosphere priming. Clearly this is a frequency-dependent, or game

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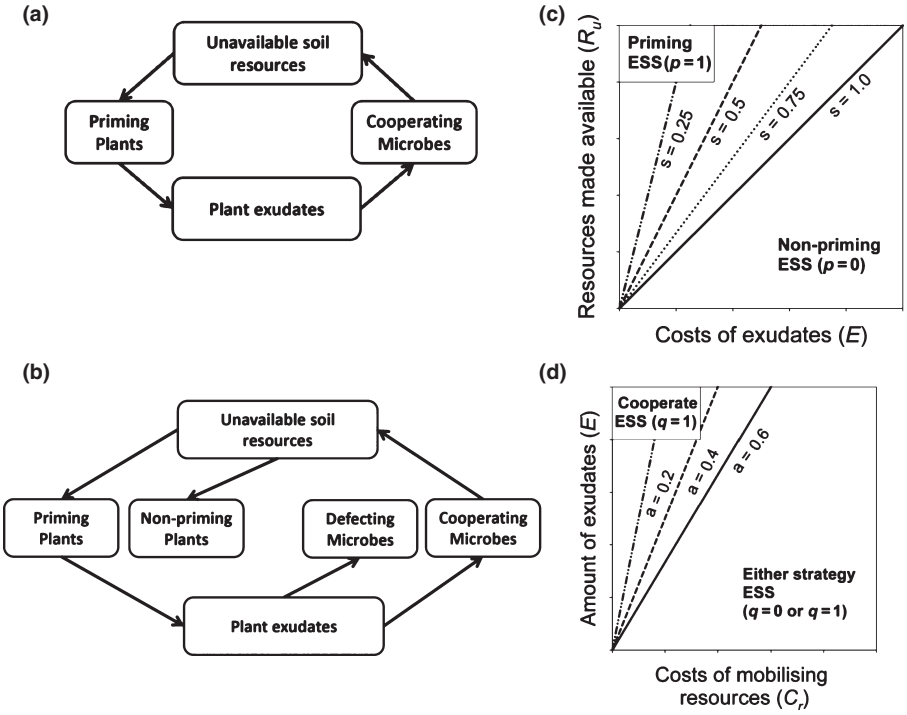

Fig. 1 Flowcharts describing (a) the typical framing of evolutionary benefits associated with soil priming by plants, where plants offer exudates to microbes and in exchange the microbes mobilize resources for plant use (e.g. nitrogen (N) or phosphorus (P) that is in a form unavailable to the plants). (b) The frequency-dependent view of soil priming. Also shown are evolutionarily stable strategy (ESS) solutions for the bimatrix game of plant–microbe coevolution. (c) Plant ESS solutions for the priming or nonpriming strategies with different levels of transaction security (s), exudate costs (E) and mobilized soil resources (R_u). For plants in this model, only pure ESSs are permissible with all plants priming ($p = 1$), or all plants not priming ($p = 0$). (d) Microbe ESS solutions for the microbe strategies of cooperate or defect with priming plants with different levels of microbe competitive ability (a). For microbes, q is the proportion of cooperating microbes in the population. Again, only pure ESSs are permissible ($q = 0$ or 1), but there is a region of alternate stable states where the microbe strategy that is favored will depend on the initial strategies contained in the system.

theoretic, scenario where the plant strategy depends on the microbe strategy and *vice versa* (McNickle & Dybzinski, 2013). Using these ideas, we developed a simple evolutionary game theoretic model that allows us to explore the simplest set of factors that may or may not favor evolution of the RPE as a coevolved mutualism (Supporting Information Notes S1). This allows us to ask two simple questions: (1) what conditions make the RPE an evolutionarily stable strategy (ESS) for plants (Fig. S1)? and (2) when is it an ESS for microbes to cooperate with priming plants (Fig. S2)?

An ESS is a strategy that cannot be invaded by a rare mutant using an alternative strategy (Smith & Price, 1973). The ESS solutions from the model can be summarized graphically (Fig. 1c). This simple model predicts that only pure plant strategies are possible, either all priming plants or all nonpriming plants. All else being equal, priming is an ESS if (1) the microbes are mineralizing nutrients in exchange for exudates; (2) the unavailable resources that the microbes make available to the plant are relatively high; (3) the relative cost of root exudates are low; and (4) the security of the transaction between plant and microbe is relatively high (Fig. 1c). The converse is true for the nonpriming strategy. The line that demarcates the evolutionary tipping point between these two strategies has a slope of $1/s$ (Fig. 1c).

For soil microbes, the ESS solutions can also be summarized graphically (Fig. 1d). With all else being equal, the cooperating strategy is favored when (1) plants provide a relatively high amount of rhizodeposits; (2) the cost of mobilizing resources for microbes is low; and (3) the security of the transaction between plants and microbes is high in terms of the ability of cooperators to capture exudates. The converse is true for defecting microbes. The line that demarcates the evolutionary tipping point between these two strategies has a slope of $1/a$ (Fig. 1d).

This model is clearly an oversimplification of reality. However, it is sufficient to make a number of basic points about the hypothesis that the RPE is a sort of *indirect* coevolved symbiotic relationship between plants and microorganisms. First, the model shows that, as hypothesized by a number of authors (Denison *et al.*, 2003; Lambers *et al.*, 2009), there are indeed conditions where such an indirect symbiosis can be favored by natural selection (Fig. 1). However, the model also suggests that this symbiosis is rather delicate and may easily shift towards a sort of parasitism. Indeed, in most regions of parameter space, the mutualism is not evolutionarily stable (i.e. nonpriming and defection are the ESSs; Fig. 1c,d). It should be noted that this game theoretic model only addresses conditions under which the RPE could have been coevolved as a mutualism. However, the model does not rule out the possibility that exudates and rhizodeposits are shed by the plant for multiple reasons and the RPE is a side effect.

The major implication of the RPE as an ESS is that conditions affecting the cost–benefit balance of the plant may alter priming intensity. For instance, the growth of plants in elevated CO_2 often

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results in more belowground C allocation, greater root biomass and increased rates of soil exploration. More C supply to roots may reduce the costs of rhizodeposits, and enhanced plant growth can increase the plant demand for soil resources, thereby favoring a priming strategy (Fig. 1c). This prediction is partially supported by the vast majority of elevated CO_2 studies, where belowground C allocation increases under conditions of high photosynthetic C supply (Pendall *et al.*, 2004; Dieleman *et al.*, 2010; Taneva & Gonzalez-Meler, 2011). If, on the other hand, the availability of mineral nutrients is high, rhizodeposition will not necessarily result in higher resource availability and both plants and microbes will be less dependent on each other's strategy, reducing priming intensity (Fig. 1c,d). This prediction is partially supported by the common decrease in soil respiration upon N fertilization in forests (Janssens *et al.*, 2010). This evolutionary game seems to support the notion that the RPE can result in an ESS by providing mutual benefits to both plants and microorganisms.

V. A microbial physiology-based model: simulating positive and negative RPEs

While most studies of the RPE have reported positive effects, several studies have also found negative RPEs (Table 1). Positive RPEs are believed to be driven by an alleviation of microbial C or energy limitation leading to increased microbial activities and demand for nutrients (Cheng & Kuzyakov, 2005). Given the faster turnover of microbes relative to plants, a positive RPE increases N mineralization and N availability to plants (Badalucco & Kuikman, 2001; Dijkstra *et al.*, 2009). By contrast, a negative RPE might occur if the utilization of labile substrates by fast-growing copiotrophic microbes reduces the activity of oligotrophic microbes involved in degrading stabilized SOC. Such a scenario could be expected in soils of low N availability, as copiotrophic microbes presumably would compete with oligotrophs for N and not C (Cheng & Kuzyakov, 2005). This mechanism is supported by a recent meta-analysis (Blagodatskaya *et al.*, 2011), which showed that adding low concentrations of labile C increased the RPE but higher concentrations of labile C decreased the RPE, as the microbial community (likely dominated by copiotrophic microbes) preferentially utilized the labile substrates (Cheng, 1999).

We performed an exploratory analysis to investigate whether a process-based model where SOM decomposition is controlled by microbial physiology (i.e. C utilization efficiency (CUE) with Michaelis–Menten kinetics) could enhance our understanding of controls on positive and negative RPEs. To do this, we modified the Allison *et al.* (2010) model to include N dynamics (using the framework of Drake *et al.*, 2013), and seasonal changes in temperature that are representative of a temperate forest (Notes S2, Figs S3, S4). The baseline model assumed constant and equal C inputs to the SOC and dissolved organic C (DOC) pools for every time step. But in our modified model, we adjusted both the timing and magnitude of inputs to the SOC and DOC pools to mimic the large litter C pulse into SOC in the fall and root C exudation into DOC throughout the growing season (Tables S1, S2).

Our modeling results indicate that differences in the physiology and traits of soil microbes can contribute to both positive and negative RPEs. For example, increasing root exudation by 20% led to a 5% decline in SOC and a 15% increase in N mineralization rates relative to the baseline (Fig. 2). However, altering microbial physiology in concert with enhanced exudation led to negative RPE, while still stimulating N mineralization rates. Two model parameters led to the shift from positive to negative RPE: increasing the amount of microbial necromass that becomes SOC and increasing the turnover rate of the microbial biomass (Fig. 2a). Increases in the amount of microbial necromass may occur in soils where the microbial CUE is enhanced; whereas an increased turnover rate of microbes may occur in soils where the microbial community shifts from being fungal-dominated to bacterial dominated. This impact of microbial physiology on the RPE is supported by a recent modeling effort, which showed that enhanced transfer of C to mycorrhizal symbionts can increase the amount of microbial necromass that enters stable SOC pools (Orwin *et al.*, 2011). Thus, emerging modeling frameworks that assimilate enzyme classes and microbial communities may hold promise for further refinement of the impacts of plant roots on SOM decomposition (e.g. Moorhead & Sinsabaugh, 2006; Moorhead *et al.*, 2012).

While our modeling exercise assumed that the RPE is driven primarily by an enhanced decomposition of biochemically stabilized C, it is critical to consider how physical protection and substrate access can influence the magnitude and direction of RPEs. Recent research is challenging the paradigm that the molecular structure of substrates and enzyme kinetics control SOC

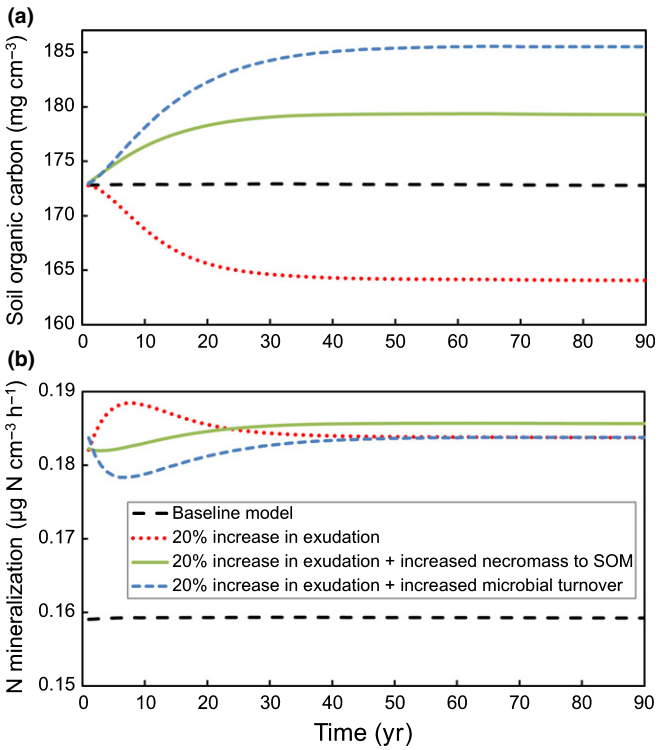

Fig. 2 Enhanced exudation is predicted to influence (a) soil organic carbon (SOC) pools and (b) nitrogen (N) mineralization rates, with the direction of these effects depending on rates of microbial turnover and the percentage of necromass assumed to become soil organic matter (SOM) for each of the three scenarios. Data presented are annual averages for SOC pools and N mineralization rates.

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decomposition and stabilization (Schmidt *et al.*, 2011). Thus, the ability of microbes to physically access substrates may be more important than the chemical quality of substrates for SOM stabilization (Schimel & Schaeffer, 2012). For example, the magnitude of the RPE may be low in soils with a high amount of aluminosilicates containing oxalate-extractable iron which may protect SOC from enzymatic degradation (Rasmussen *et al.*, 2007). In terms of physical protection within soil aggregates, the magnitude and direction of the RPE will likely depend on whether rhizosphere processes break up (or form) aggregates, thereby affecting microbial access to occluded particulate organic matter or to SOC protected in fine-scale pores (McCarthy *et al.*, 2008; O'Brien & Jastrow, 2013). For positive RPEs, the rhizosphere can be envisioned as a moving front where root-derived C is transferred by the foraging of roots and mycorrhizae to soil volumes that were previously inaccessible. This movement of the rhizosphere increases SOC decomposition by alleviating both chemical and physical barriers. In the two model scenarios with negative RPEs (Fig. 2), exudation enhanced microbial biomass and increased the amount of necromass transferred to stable SOC. These scenarios are not incompatible with physical protection as it is implicit in a greater transfer of microbial derived products to SOC (Grandy & Neff, 2008).

Collectively, these results indicate that an improved understanding of the role of microbial physiology (e.g. CUE, microbial turnover) in response to labile C inputs will be critical for representing these dynamics accurately in models. As currently formulated, Earth system models lack the ability to incorporate the RPE because SOM decomposition is solely a function of first-order rate constants and soil microbes are modeled as a C pool that has no function or physiology (Todd-Brown *et al.*, 2013). Overall, our modeling results suggest that including root dynamics and microbial physiology into Earth system models will likely change how C and N are cycled in these models.

VI. A case study: matching simulation results with observations at the Duke FACE

Numerous studies have shown that the RPE can impact the decay rate of different SOM pools (Kuzyakov, 2002; Finzi *et al.*, 2006; Phillips *et al.*, 2011; Shahzad *et al.*, 2012). In this section, we evaluate the potential impact of the RPE on ecosystem dynamics for the elevated CO_2 treatment at the Duke FACE site. The observed plant production and nutrient cycling datasets show that plant N uptake and production increased under elevated CO_2 compared to the ambient CO_2 treatment (McCarthy *et al.*, 2010; Drake *et al.*, 2011), and these increases were sustained throughout the entire experimental time period (15 yr). Several papers suggest that the primary biological mechanism for the increase in plant N uptake was the RPE (Pritchard *et al.*, 2008a,b; Phillips *et al.*, 2011, 2012). The observed data sets from Duke show that root production, root respiration rates and total soil respiration rates increased by up to 30% for the elevated CO_2 treatment and support the idea that increased belowground C allocation enhanced priming effects (Drake *et al.*, 2008, 2011; Jackson *et al.*, 2009). This idea is further supported by isotope data. The constant isotopic label applied via the fossil-fuel source of CO_2 used for CO_2 enrichment can track and separate recent photosynthate from stored SOC in soil respiration fluxes (Andrews *et al.*, 1999), and during the first year of enrichment most of this labeled C represents root–rhizosphere respiration (due to the slow turnover of leaves and roots; Matamala *et al.*, 2003). In 1997 and 1998, soil respiration in the elevated CO_2 treatment increased by 220 g C m^{-2} yr^{-1} compared to the ambient CO_2 treatment (Hopkins *et al.*, 2013). Post-enrichment C contributed only 140 g C m^{-2} yr^{-1} of the increase; the remainder was due to an increase in mineralization of pre-existing SOM. Therefore, 31% of the increase in soil respiration during the first years of the experiment was due to accelerated mineralization of existing SOM, likely the result of the RPE which may have been sustained over later years (Taneva & Gonzalez-Meler, 2011). In this modeling exercise, we evaluated the potential ecosystem impact of the RPE by increasing the decay rates of the microbial biomass, the slow SOM pool (turnover time ranges 10–30 yr), and the passive SOM pool (turnover time > 1000 yr) in the PhotoCent ecosystem model (Savage *et al.*, 2013).

The PhotoCent model is a revised version of the ForCent model (Parton *et al.*, 2010) and includes a simplified version of the Farquhar photosynthesis model (Aber & Federer, 1992). The PhotoCent model was first set up to simulate the ambient and elevated CO_2 treatments at the Duke FACE site without considering the RPE on ecosystem dynamics. Next, we simulated the ecosystem impacts of the RPE in the elevated CO_2 treatment by assuming decay rate increases for the microbial, slow and passive SOM pools of + 10%, + 30% and + 50%, respectively. We chose this range because the observed increases in root production and total soil respiration rates could reach 30% under the elevated CO_2 treatment (McCarthy *et al.*, 2010; Drake *et al.*, 2011). We then compared the model-simulated impact of elevated CO_2 on average annual (1996–2004) plant production, plant N uptake and SOC with observed data from the site.

When the RPE was not included, the model underestimated the observed increase in plant production and plant N uptake under elevated CO_2 (Table 2). However, when the model was run with enhanced decay rates for the elevated CO_2 treatment, both plant production and N uptake were higher as a result of increasing the decay rate of the slow SOM pool, but increasing the decay rates of the microbial and passive pools had little impact on plant production and N uptake. As expected, the C contents of the different SOM pools were lowered by increasing their decay rates, and increasing the decay rate of the slow SOM pool caused the largest reduction in total soil C.

The simulated priming model results suggest that increased plant production and N uptake are sustained when priming of the slow SOM pool (enhanced decay) occurs. These results demonstrate that the PhotoCent model benefits from including the RPE – enabling it to correctly simulate the observed increases in plant production and N uptake for the elevated CO_2 treatment. Consistent with observations, the model simulated little change in SOM content for the elevated CO_2 treatment (Drake *et al.*, 2011). By contrast, without including the RPE, the model predicted increases in SOM content. Thus, accelerated turnover of the slow SOM pool as a consequence of the RPE is a potential mechanism whereby total

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Table 2 Results of model simulations with increased decay rates for different soil organic matter (SOM) pools because of the rhizosphere priming effect (RPE)

	RPE	Plant production	Plant N uptake	Total SOC	SOC microbe	SOC slow	SOC passive
Observed		1128	10	3103			
No RPE*	0%	930	8.19	3260	51.0	1510	1700
Microbial	10%	933	8.21	3260	46.5	1510	1700
	30%	937	8.25	3250	39.5	1510	1700
	50%	940	8.28	3250	34.2	1520	1700
Slow	10%	985	8.57	3220	53.8	1470	1700
	30%	1090	9.27	3150	59.0	1390	1700
	50%	1170	9.88	3080	63.3	1320	1700
Passive	10%	932	8.21	3260	51.1	1510	1700
	30%	938	8.24	3260	51.2	1510	1700
	50%	944	8.28	3250	51.4	1510	1690

Increased decay rate for slow SOM pool by 40% resulted in best matches between model output and observed results in terms of plant production, plant N uptake, and total soil C content. Observed plant production is from McCarthy *et al.* (2010), and plant N uptake and total SOC are from Drake *et al.* (2011). The unit is g C m^{-2} for all SOC pools, and g C or N m^{-2} yr^{-1} for plant production and N uptake.
*Assuming no extra rhizosphere priming under elevated CO_2 as compared to the ambient CO_2 treatment.

SOC storage can remain unchanged despite an increase in belowground C inputs as observed under elevated CO_2 at the Duke FACE site (Finzi *et al.*, 2007; Jackson *et al.*, 2009; Drake *et al.*, 2011).

This case study demonstrates how incorporating the RPE into the PhotoCent model can significantly improve model performance, even though base-level RPE was already implicitly included in the decay rates of the SOM pools for the ambient conditions during model calibration. In this case, the extra RPE and its effect on SOM decomposition rate (*c.* 40% greater for the slow pool) in the elevated CO_2 treatment was critical for explaining sustained increases in plant production and plant N uptake amounts, as well as the lack of change in SOC stocks. Similar phenomena were seen at two other FACE sites (Allard *et al.*, 2006; Talhelm *et al.*, 2009) where elevated CO_2 enhanced NPP but resulted in a decline in SOC. By contrast, at the Oak Ridge FACE site, SOC increased when elevated CO_2 enhanced NPP to a similar degree (Jastrow *et al.*, 2005; Norby *et al.*, 2005; Iversen *et al.*, 2012). This inconsistency in SOC balance among FACE experiments is understandable, given that soil C status can be controlled by many other factors, for example, C partitioning (DeLucia *et al.*, 2005), C–N interactions (Hungate *et al.*, 2009; Dieleman *et al.*, 2010), physicochemical protection (Jastrow *et al.*, 2005) and bioturbation (Hoosbeek & Scarascia-Mugnozza, 2009), in addition to NPP and priming. These factors have been shown to control and modulate both soil C gain through stabilization of the extra C input from CO_2 fertilization (Jastrow *et al.*, 2005) and C loss through the increases in microbial mineralization of SOM via the RPE (Drake *et al.*, 2011; Norby & Zak, 2011). Thus, elevated CO_2 may enhance both C gain and C loss from SOM, but the net balance may differ for different forest ecosystems, thereby resulting in no change, net loss or net gain in global SOC stocks (Billings *et al.*, 2010; Dieleman *et al.*, 2010). However, the intensity of the RPE implicated in some of these field experiments was largely unexpected, because most current ecosystem models (Manzoni & Porporato, 2009) predict some gain in SOC under elevated CO_2 that is largely driven by the increase in NPP. Our case study and results from other studies clearly illustrate the need to incorporate the RPE into these models because the close link between C input and the RPE can qualitatively change model performance (Wutzler & Reichstein, 2013).

VII. Research needs and future perspectives

Research on the RPE is still at an early stage, and many crucial questions remain open (Gärdenäs *et al.*, 2011). As discussed in the previous sections, the RPE, as a key mechanism, can be controlled and influenced by plant, soil and climate variables (Fig. 3). Comprehensive understanding of the RPE and related future model development requires thorough integration of all important variables. However, at the current stage such integration is highly challenging because our basic understanding is limited.

Among plant variables, photosynthesis, NPP and species are closely connected to the RPE. Yet, many critical questions remain to be addressed. For instance, at the physiological level, we do not know whether plants have built-in physiological mechanisms for actively controlling the RPE or to what degree the RPE is controlled by plant physiology. These questions demand future close collaborations

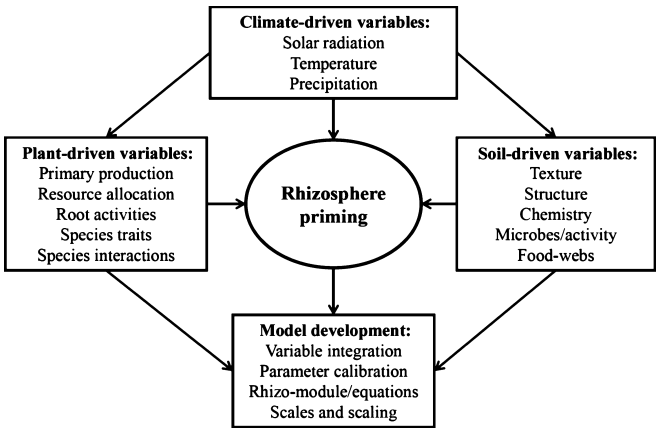

Fig. 3 A conceptual framework connecting three sets of variables that interact to control rhizosphere priming effects with modeling approaches needed to reliably incorporate these variables into future models.

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between plant physiologists and soil ecologists. At the interspecific level, mixtures of plant species have been shown to dampen the RPE compared to the average in monoculture (Dijkstra *et al.*, 2010; Pausch *et al.*, 2013). But we have little information about the consistency of this response in terms of direction or magnitude for different plant communities or the mechanisms by which interspecific interactions alter the RPE. Even less is known about the RPE at the ecosystem level. Although C input to the rhizosphere may be the primary driver of the RPE, it is crucial to discover the quantitative relationships between rhizosphere priming intensity and the amounts of C allocated to roots, rhizosymbionts and rhizodeposits (including exudates) in an ecosystem. Another high priority for research is the need to investigate how the RPE is regulated in different ecosystems. Do plants regulate the RPE by specifically controlling rhizospheric microbial partners (such as selecting the type and the quantity of mycorrhizal fungi)? Furthermore, current understanding of the RPE is based primarily on results obtained from laboratory experiments or highly disturbed systems and, therefore, not directly applicable to natural or most managed ecosystems. To date, little is known about the RPE under realistic field conditions, except that elevated atmospheric CO_2 concentrations may significantly enhance the RPE, primarily due to substantial increases in NPP as demonstrated in some FACE experiments. Investigating the RPE under realistic field conditions is clearly a priority for future research.

Among soil variables, nutrient availability (Cheng & Johnson, 1998), soil water content (Dijkstra & Cheng, 2007b), temperature (Zhu & Cheng, 2011), rhizosphere microbial associations (Fontaine *et al.*, 2011; Cheng *et al.*, 2012), and exoenzymes (Phillips *et al.*, 2011; Zhu & Cheng, 2011) have been shown to significantly affect the RPE. However, the actual mechanisms behind these effects are virtually unknown. For example, we do not know whether soil nutrients affect the RPE by altering plant C allocation, by modifying the stoichiometry of soil microbial communities, or by modulating rhizosphere chemistry. Nor do we know the precise relationships between the RPE and key variables such as soil temperature and moisture or how soil properties such as mineralogy, texture and structure might influence the RPE. Some exploratory hypotheses were given in a past review (Cheng & Kuzyakov, 2005), but empirical testing of those hypotheses has rarely been performed. Soil microbial metabolism (e.g. substrate utilization and exoenzyme production) has been hypothesized as the central mechanism responsible for controlling priming effects (see Allison *et al.*, 2010; Blagodatsky *et al.*, 2010), and this hypothesis has been incorporated into simulation models with promising results (Neill & Gignoux, 2006; Wang *et al.*, 2013). Similarly, our exploration of a simple soil microbial physiology-based model demonstrated how the timing, quantity and quality of C inputs affects the RPE and its impact on soil C and N pools. But theoretical formulations coupled with empirical data are still lacking. Microbial community succession (e.g. from r- to K-strategy) has also been hypothesized as a mechanism behind priming effects (Fontaine *et al.*, 2003). This hypothesis is rooted in the fact that the rhizosphere environment selects for distinctive groups of microbes (DeAngelis *et al.*, 2009) and that the composition of the rhizosphere microbial community undergoes a series of successional stages as fine roots grow through the soil matrix and then senesce and turn over. However, it is still difficult to ascertain whether rhizosphere microbial succession is the cause of the RPE or the consequence of the RPE.

Another key hypothesis emphasizes the role of rhizosphere-driven turnover of soil aggregates (Cheng & Kuzyakov, 2005). Because roots promote the reorganization of soil structure, they can destroy existing aggregates possibly by intensifying drying–wetting cycles (Zhu & Cheng, 2013) and also enhance the formation of new ones via physical entanglement and the production of cementing agents such as mycorrhizal and microbial metabolites (Haynes & Beare, 1997; Jastrow *et al.*, 1998). Accelerated aggregate turnover releases substrates that were previously inaccessible because of occlusion within aggregates, and also concurrently stabilizes and protects new substrates from microbial mineralization in newly formed aggregates (Tisdall & Oades, 1982; Elliott, 1986; Beare *et al.*, 1994; Plante & McGill, 2002). This aggregate turnover hypothesis aligns well with the emerging view of the drivers promoting SOM stabilization (Schmidt *et al.*, 2011), which emphasizes the roles of physicochemical protection and biological accessibility, and downplays the role of molecular structure and biochemical recalcitrance. However, simultaneous measurements of the RPE and soil aggregate dynamics will be needed to validate this hypothesis in future research.

As summarized earlier, the RPE is likely responsive to global change factors – such as elevated atmospheric CO_2 concentrations, warming and N deposition – because environmental variables impact both plant and soil components (Fig. 3). However, very little is known about how these environmental variables actually affect the RPE or how to mathematically describe the quantitative relationships between the RPE and these variables. Furthermore, we need to determine whether it is necessary to parse out the effects of environmental variables on plant and soil variables and their interactions for the RPE to be accurately understood. The reason for seeking answers to these questions can be illustrated by the outcome of our case study of the Duke FACE experiment. We demonstrated that it was necessary to include a RPE that stimulated a 40% increase in the decomposition rate of the slow SOM pool in the PhotoCent model to more accurately match model output with observed data. If this increase in intensity of the RPE is solely driven by the 30% increase in root C input observed in the elevated CO_2 treatment at the Duke site, then perhaps the RPE can be incorporated in general models once we know the mathematical equations that determine the RPE. For example, it might be reasonable to assume that the RPE is some function of the rate of root C input, that is, $RPE = f(C_root)$, where C_root is the rate of root C input (for the sake of simplicity). However, considerable work will be needed to determine whether this general relationship holds for different ecosystems across space and time and, if so, to acquire the observational data needed to formulate mathematical equations that can describe the effects of environmental variables on the relationship.

Recognition of the magnitude and the significance of the RPE warrants incorporation of the RPE into models at the ecosystem level and larger scales (Guenet *et al.*, 2010; Wutzler & Reichstein, 2013). However, at present, integrating the RPE and its

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modulation by all three sets of variables (plant, soil & environment) into ecosystem models seems a daunting task. To move forward, we recommend three approaches for future research. The first approach is to insert a set of RPE-related parameters into existing models for the purpose of testing the sensitivities of model performance to these parameters in a variety of ecosystems under differing conditions. By doing so, we can explore the potential significance of each parameter, which will help us set research priorities and generate testable research hypotheses. Our case study of the Duke FACE experiment is an example of this approach, which clearly tied the RPE with an increase in the decay rate of the slow SOM pool under elevated CO_2. The second approach is to develop mathematical equations and simulation modules specifically for quantifying the RPE. The emphasis of this approach should be on developing quantitative relationships between the RPE and its controlling variables. These equations and modules can be used as building blocks for future ecosystem and Earth system models (e.g. Wutzler & Reichstein, 2013). The third approach is to search for scaling relationships between the RPE and other variables that are easier to quantify or already have a usable database. This approach requires an adequate level of data accumulation for both the RPE and other potentially scalable variables.

Inevitably, all three approaches will still have to confront the widely known rhizosphere complexity, derived from the innate spatial and temporal heterogeneity and the high degree of connectedness that occurs in the rhizosphere (Hinsinger *et al.*, 2005). Regardless, to face the multi-faceted challenges of properly incorporating the RPE into ecosystem and Earth system models, close collaboration and feedback between researchers interested in model development and researchers interested in obtaining model-usable empirical data is a meaningful first step for moving forward.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Plant payoff matrix.

Fig. S2 Microbe payoff matrix.

Fig. S3 Seasonal variation in soil temperature at 5 cm depth for 2011 at the Morgan Monroe State Forest AmeriFlux site, IN, USA.

Fig. S4 Seasonal fluctuation in the size of the SOC pool for the first 30 yr of the baseline model simulation.

Table S1 Baseline model parameters modified from Allison *et al.* (2010)

Table S2 Parameter modifications from the baseline model for the three scenarios

Notes S1 Detailed descriptions of the game theoretic model.

Notes S2 Detailed descriptions of the microbial physiological model.

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